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MANGROVE POLLEN AT THE DEPOSITIONAL SITE OF OLIGO-MIOCENE AMBER FROM CHIAPAS, MEXICO¹

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AMBER from the New World tropics has been reported to occur in Mexico, Colombia, Brazil, Argentina, Haiti and the Dominican Republic (Langenheim, 1964). Neither the amber itself nor the environment of its deposition in any of these localities, however, has previously been studied in detail.

¹ Grateful acknowledgment is expressed to Prof. J. Wyatt Durham and Prof. E. S. Barghoorn for continued interest and help with the project as well as criticism of the manuscript. The critical comments of Prof. A. O. Dahl and Dr. Lucy Cranwell Smith are also appreciated. The investigation was supported in part by National Science Foundation grants GB 1312 and 2397, and the Radcliffe Institute for Independent Study.

² The senior author was a Research Associate in the Botanical Museum, now at the University of California at Santa Cruz. Miss Hackner, now at the University of Pennsylvania, investigated the mangrove and associated fossil pollen in the Chiapas amber-bearing sediments for a Senior Thesis at Radcliffe College under the supervision of Dr. Langenheim. Miss Hackner gratefully acknowledges support of this study by an National Science Foundation Undergraduate Research Participation grant. Dr. Bartlett, Harvard University, made a special study of modern *Rhizophora* and other tropical pollen in connection with this project and with her present studies of Late and Post-Glacial history of Gatun Basin, Panama. She wishes to express appreciation to the American Chemical Society, PRF Grant 947-A-2, for assistance in this study.

The classic concept of amber has been derived from the extensive deposits along the shores of the Baltic Sea which have been rather intensively studied for over a century. This Baltic amber is known to have been produced in forests with a high proportion of subtropical to tropical floral and faunal elements (Czeczott, 1960; Schubert, 1958; 1961). Yet most comparative observations of resin-producing trees and the manner in which they produced large quantities of resin that could be deposited in the sedimentary record were restricted to cool temperate conditions around the Baltic Coast. Much emphasis was placed on the necessity for an extensive forest of trees producing resin excessively in response to diseased and physiological imbalance in order to accumulate the incredible deposits that occur along the Baltic coast (Conwentz, 1890). Little attention was given to the fact that tropical trees can produce large quantities of resin under apparently natural forest conditions and that environments of deposition occur there that can favor large accumulations of resin. Unfortunately, it has been impossible to study the primary environment of deposition of the Baltic amber, because it is thought to be secondarily deposited (Czeczott, 1960).

Amber from the Simojovel region, Chiapas, Mexico, is one of the occurrences in the New World tropics that provides sufficiently abundant material for detailed investigation. Entomologists from the University of California at Berkeley became aware of the presence of numerous insects in this amber and initiated a collecting and study program in 1953 (Hurd and Smith, 1957). Although the occurrence of this amber has been recorded since at least 1891, the extent of the deposits and potential biological significance of the material had not been known. The inaccessibility of this area in the southernmost state of Mexico and the possessive attitudes of the

natives there toward the amber probably also contributed to lack of previous recognition. Invertebrate paleontologists at Berkeley since 1956 and stratigraphers at the University of Illinois since 1961 have been studying the geology of the amber-bearing beds in the Simojovel region in order to establish the age of deposition of the amber as a context for evolutionary studies of the included fossils. Various phases of botanical investigations of the amber and of the beds containing it were begun in 1962 at Harvard University and extended to include chemical aspects in 1963. Thus, the study of the Chiapas amber has been approached from the standpoint of coordinating data from several disciplines that may shed light on mid-Tertiary ecosystems in southern Mexico. It has, furthermore, provided an opportunity to understand more fully the natural production of large quantities of resin and sites that favor its accumulation and subsequent deposition in sediments under tropical conditions.

Pollen analysis of the Chiapas amber-bearing beds is of particular interest in any attempt to determine some of the vegetational and general environmental conditions that could have existed at or near the site of deposition of the amber. Study of 12 samples from amber-bearing strata in various localities indicates that the primary depositional environment of the amber was dominated by mangrove vegetation comprised of several species of *Rhizophora*. Although numerous other microspore types occur in these sediments, this report will be restricted essentially to a discussion of *Rhizophora*, with brief mention of associated pollen types which were strikingly abundant or otherwise significant to an understanding of the ecology of vegetation at or near the depositional sites of the Chiapas amber. The record of occurrence of *Rhizophora* pollen in these strata contributes also to our knowledge of the distribution and ecology of mangrove

vegetation during the mid-Tertiary in southern North America.

BOTANICAL SOURCE OF THE AMBER

In contrast to the classical view that amber is derived from pines or, at least, pines and other conifers, it has been demonstrated on the basis of several lines of collateral evidence that the source of most of the Chiapas amber is the leguminous genus *Hymenaea* (Langenheim and Beck, 1965; Langenheim, 1966). This genus has the center of its distribution today in the Amazon Basin. Of the 20 species commonly recognized (Record and Hess, 1943), only one species,³ *Hymenaea Courbaril* L., has a wide distribution. It occurs throughout northern South America (Brazil, Bolivia, Colombia, Ecuador, Venezuela, the Guianas), along the Pacific slopes throughout Central America to central Mexico, and on most of the islands of the West Indies. Prof. Faustino Miranda (per. comm., 1964) identified a *Hymenaea* leaflet in the amber which resembles both *H. Courbaril* and *H. intermedia* Ducke, the latter today restricted to the Amazon region. On the basis of diagnostic glandular morphology, the leaflet probably more closely resembles present-day populations of *H. Courbaril* than *H. intermedia*. Likewise, similarities in the infrared spectra of most of the Chiapas amber and of resin of modern populations of *H. Courbaril* make it appear that the amber was produced possibly by an ancestral population of *H. Courbaril*.

Although ecological data are scarce throughout its wide range of distribution, the senior author has observed *Hymenaea Courbaril* to be an important member

³ Some taxonomists also recognize *Hymenaea candolleana* HBK. as occurring in Central America. Most workers, in Mexico at least (F. Miranda, per. comm. 1964), think that *H. candolleana* is at best a variety of *H. Courbaril* and does not warrant specific designation.

of humid evergreen or of seasonally dry semi-deciduous forest types on the Pacific slopes in Central America. It is common along coastal plains and rivers, and grows also on beaches and sandy ridges that interdigitate with lagoons. *Hymenaea Courbaril* varies in the amount of resin produced under natural forest conditions at various sites. It appears to produce larger quantities where conditions favor a more rapid growth rate. Resin may accumulate in the soil around the base of the tree in large amounts (Noriega, 1918; Record and Hess, 1943) and from there can easily be transported into either marine or brackish-water sites in or near which mangroves frequently predominate.

GEOLOGICAL OCCURRENCE OF THE AMBER

The Simojovel Area is located in central Chiapas in the Central Mesa region and parts of the Tabasco Coastal Plain. The amber is collected primarily from rocks exposed in landslides (Plate XXXVIII), although some outcrops of beds containing amber occur along river banks and in road cuts.

Although geological investigations of the amber-bearing beds were begun in 1956, little detailed stratigraphic information has yet been published. Licari (1960), in a preliminary study of the region, described the largely Oligocene Simojovel Group as consisting of approximately 6550 feet of well-bedded marine calcareous sandstones and mudstones with some intercalated lignitic seams. It is underlain by Eocene sandstones, shales and conglomerates and overlain by Miocene sandstones and shales. The upper portion of the Simojovel Group, including a distinctive limestone member, is characterized by the presence of the marine gastropod genus *Orthaulax*, indicative of late Oligocene to earliest Miocene age. Amber has been found in the "*Orthaulax*

zone'' and in the lowermost part of the overlying sandstones and shales.

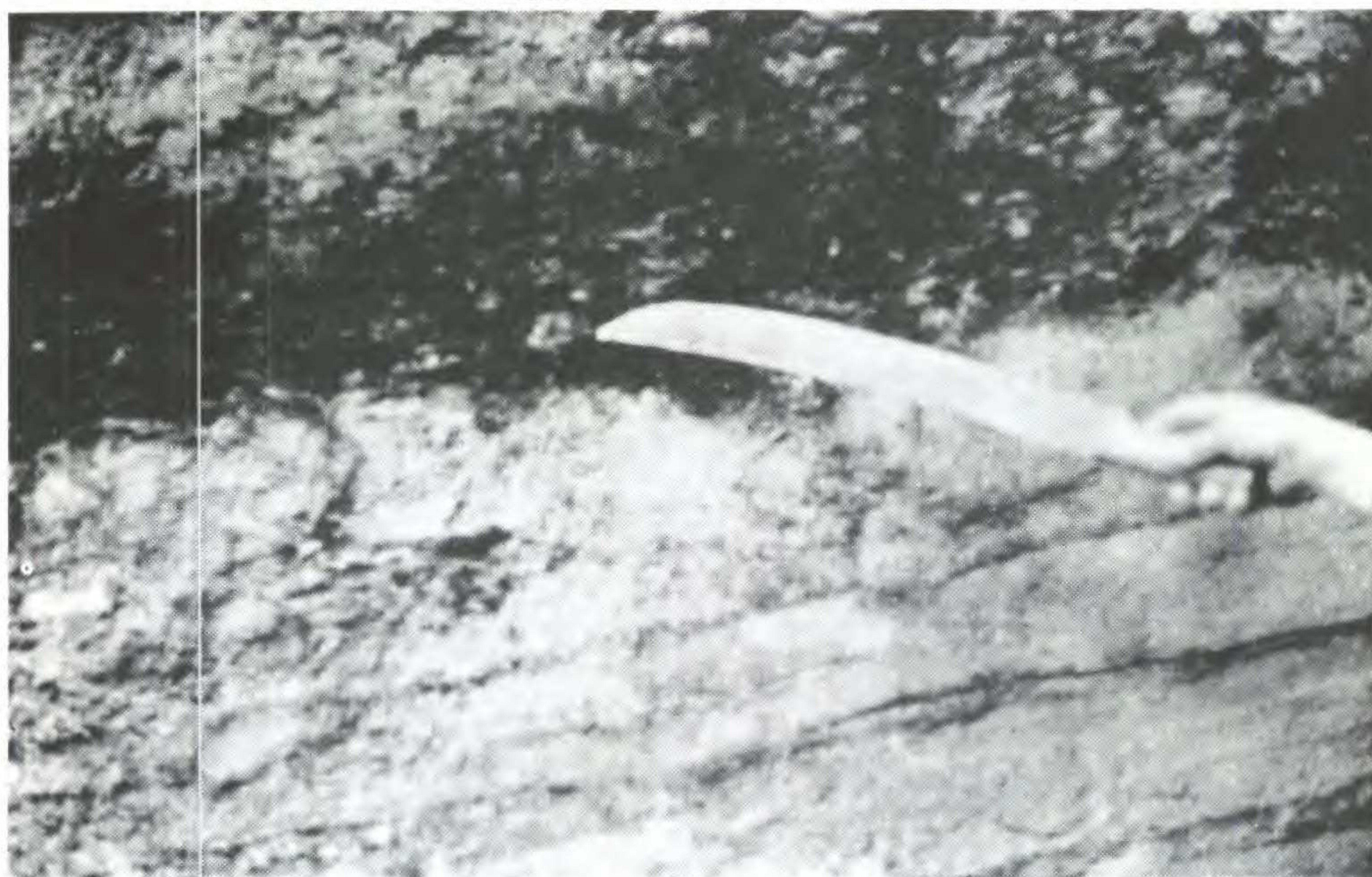
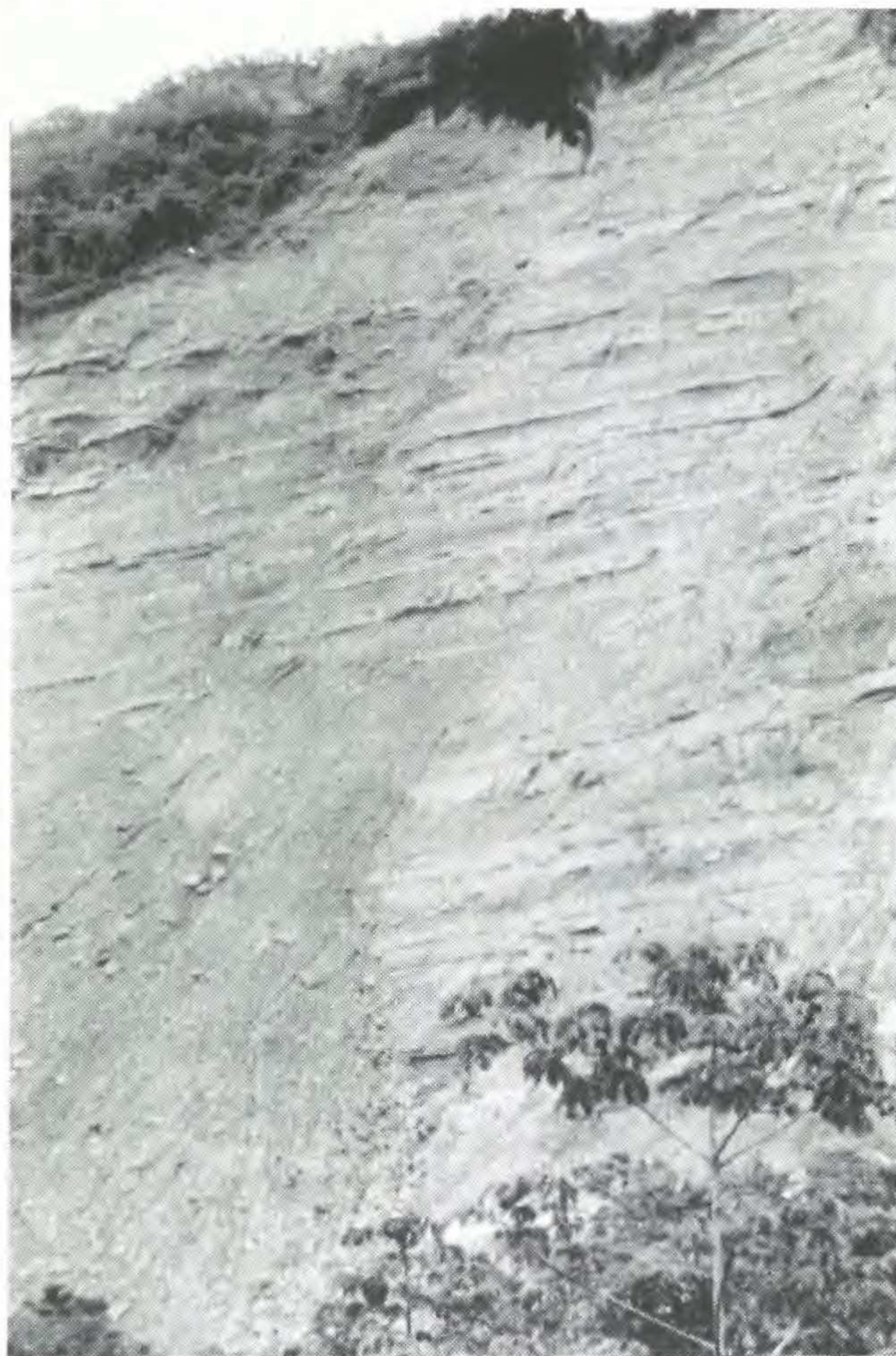
The geologic history inferred for the Simojovel Group suggests deposition of sediments, derived from the ancestral Sierra Madre to the south, under warm, generally shallow-marine conditions. Occasional shoreline oscillations led to deposition in terrestrial, estuarine and brackish environments.

DESCRIPTION OF SAMPLES FOR POLLEN ANALYSIS

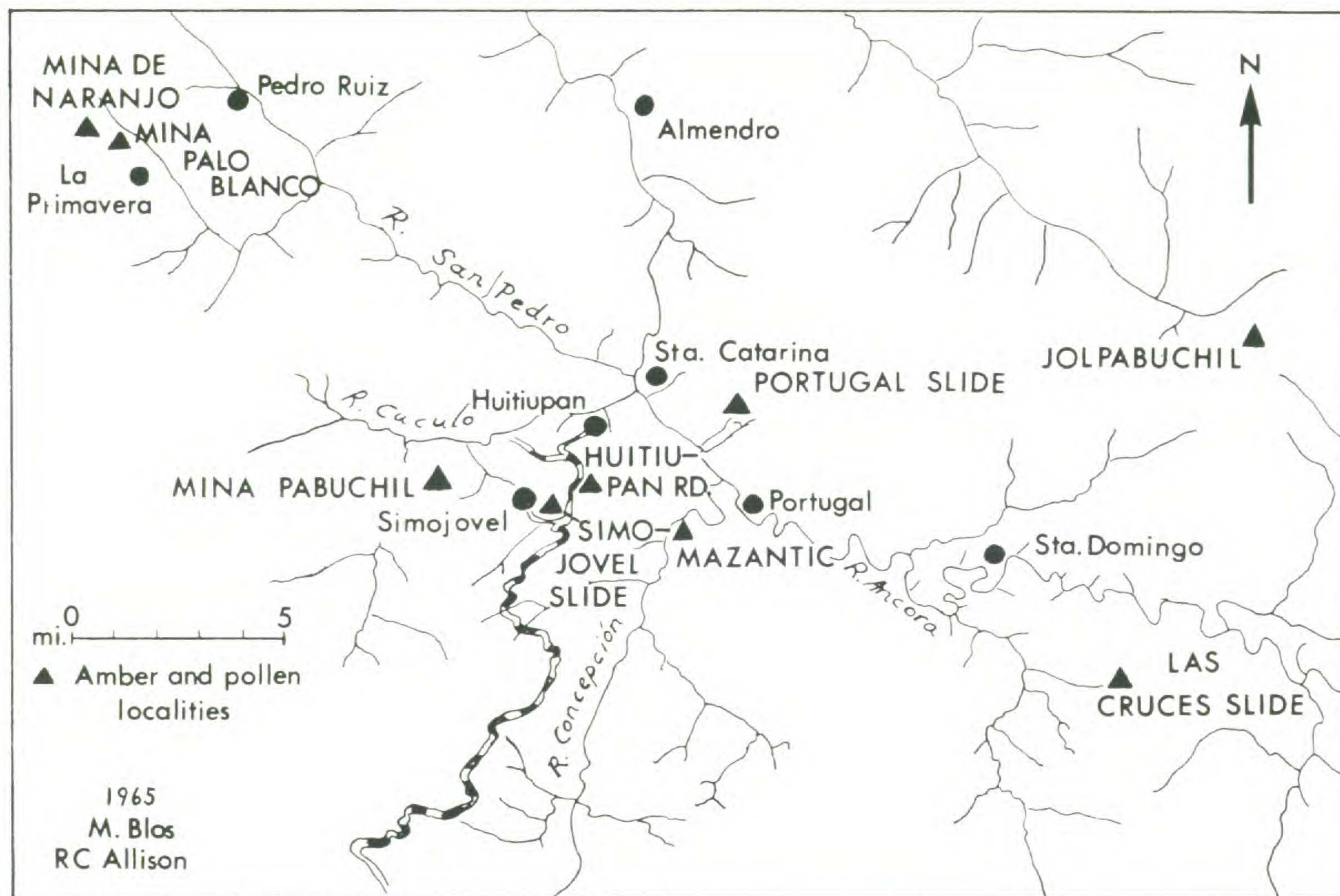
The samples analysed for pollen were collected by J. Wyatt Durham and Jean H. Langenheim from beds in which the amber occurred or from immediately adjacent beds (Plate XXXVIII). In general, the amber from these deposits does not appear to be reworked; hence it may be possible to determine some of the vegetational conditions at or near the depositional site. Location of sites from which samples were studied are indicated in Plate XXXIX. Lithologic description of the 12 samples is presented in the Appendix. Most of the samples were either calcareous siltstones or silty shales, three of the latter being glauconitic. There was some variation in coarseness and in color. One sample was a calcareous sandstone. Several samples were associated with lignitic bands or at least had carbonaceous streaks.

All of the samples are from the upper portion of the Simojovel Group and of latest Oligocene or earliest Miocene age (Durham *in lit.*, 1964). Samples from Simojovel, Mazantic, Pabuchil, Huitiupan, Portugal and Las Cruces (I–VII) are believed to be of approximately the same age (Durham, pers. comm. 1965). Durham also indicated that stratigraphic control on Sample XII from Jolpabuchil has not been established. R. C. Allison (*in lit.* to Durham) considers the invertebrate fauna from Mina Palo Blanco and Mina de Naranjo to indicate an

PLATE XXXVIII



(Top) Las Cruces landslide showing alternation of marine siltstones and sandstones with some intercalated brackish water sediments.
(Bottom) Amber deposited in lignitic bed among marine sandstones, Simojovel landslide.



Location of sites where pollen samples were collected in association with amber, Simojovel Area, Mexico.

age similar to that of Simojovel, Portugal and Jolpabuchil. Thus, available information suggests that the present samples represent a geologically short time interval.

DETERMINATION OF RHIZOPHORA POLLEN

Preparation Procedures

The pollen samples were prepared by techniques modified from various standard sources (Faegri and Iversen, 1964; USGS Prep. Proc., 1960; Brown, 1960) in a manner found suitable in the treatment of sediments of this type in other investigations at the Paleobotanical Laboratories of the Botanical Museum of Harvard University. Samples were first disaggregated by soaking in distilled water and by gentle grinding in a mortar with a pestle. The major portion of calcareous material was removed with 10% HCl; then lignin was removed by bleaching in acidified 7% NaClO₂. Larger quartz grains and other heavy minerals were removed by heavy-liquid separation in a solution of ZnBr₂ in 10% HCl at a specific gravity of 2.2. Finer silicious material was dissolved by overnight soaking of the sample in concentrated HF, followed by washing in HCl to minimize silica gel formation. The samples were acetolysed to remove remaining cellulose, and mounted in glycerin jelly.

The fossil pollen types were identified by comparison with modern pollen in the Harvard Pollen Collection. Additional modern samples prepared for this study were treated by standard methods used for this collection: i.e., treatment in hot 10% KOH followed by acetolysis and mounting in glycerin jelly.

Modern Rhizophora pollen

The genus *Rhizophora* was monographed by Salvoza in 1936, and was reviewed by Hou in 1960. Salvoza recognized *R. Mangle* L. and *R. samoensis* (Hochr.)

Salvoza as separate species, mainly on the basis of their geographical separation into two groups living respectively on the east and west coasts of America, and because of a difference in length of style. Salvoza also recognized *R. brevistyla* Salvoza on the Pacific coast as a species distinct from *R. Harrisonii* Leechm. on the east coast of America, chiefly on the basis of a difference in flower and flower-bud size and difference in stylar length. Hou does not think that the difference between the two groups in each pair is sufficient to warrant specific designation. He recognizes only three American species: *R. Mangle* L., *R. Harrisonii* Leechm., and *R. racemosa* G. F. W. Meyer. Of these, only *R. racemosa* has not yet been found on the Pacific coast of the Americas, the other two occurring on both coasts.

Pollen of the various New World species of *Rhizophora* had previously not been studied in detail. Van der Hammen (1963; pers. comm., 1965) has expressed the opinion that pollen of the three species of *Rhizophora* occurring today in British Guiana can be distinguished morphologically, but he does not separate them in his data. Muller (1959) observes that pollen of the *Rhizophora*-type shows "rather strong variation in size and in the appearance of pores." He attributes this variation, however, to difference in preservation rather than to morphological distinction of value in separation of the species.

Observations of modern *Rhizophora* pollen by the authors have led them to concur with van der Hammen that the species of *Rhizophora* can be separated in some cases by morphological characters, and an attempt to do so will be made in this paper.

The following description of pollen of several species of modern *Rhizophora* is presented after study of the *Rhizophora* pollen available from specimens in the Harvard University Herbaria and from the Harvard Pollen Collec-

tion. All size measurements are of the greatest dimension.

Rhizophora L.⁴ Grains from 11 to 30 μ in size, varying in shape from subprolate to spheroidal to suboblate. Polar view circular to triangular in grains with gaping colpi. Tricolporate; ectexinous colpi crossed by colpi transversales or elongated into a colpus aequatorialis. Colpi transversales costate to varying degrees at edges. Exine less than 1 to ca. 2.5 μ thick. Ectexine generally thinner than endexine except sometimes at poles. Ectexine varies from smooth with very indistinct pattern to scabrate with distinct columellae.

1. *R. Mangle* L.: Grains 11–28 μ , spheroidal to subprolate; circular to triangular in polar view. Shape generally well-defined and very regular, ranging from circular to oval with a slight equatorial bulge in equatorial view. Costae transversales well developed. Small grains psilate; exines of large grains scabrate with distinct columellae forming regular patterning in surface view. Colpi transversales of medium width. Plate XL, fig. 3.

2. *R. samoensis* Salv.: Grains 14–28 μ , subprolate; nearly rhomboidal in equatorial view; grains mostly well formed, regular in shape. Costae colpi and costae transversales very narrow. Ectexinous colpi constricted at junction with colpus transversalis. Columellae not so distinct as in *R. Mangle*; ectexine psilate to very finely scabrate. Ectexine heavier at poles.

3. *R. racemosa* G. F. W. Meyer: Grains 15–26 μ in breadth, typically oblate-spheroidal to suboblate; colpi transversales very narrow, often ragged. Grains tend to crumple more than do those of *R. Mangle* L. Ectexine psilate and appearing almost structureless in most grains. Surface pattern indistinct. Plate XL, figs. 1 and 7.

4. *R. Harrisonii* Leechm.: This description does not

⁴ Terminology from Erdtman (1952) and Faegri and Iversen (1964).

include the *R. brevistyla*-type, as none were recognized in this fossil assemblage. Pollen 12–24 μ . Grains are generally ill-formed, tending to crumple easily. Shape, size, and sculpturing very variable.

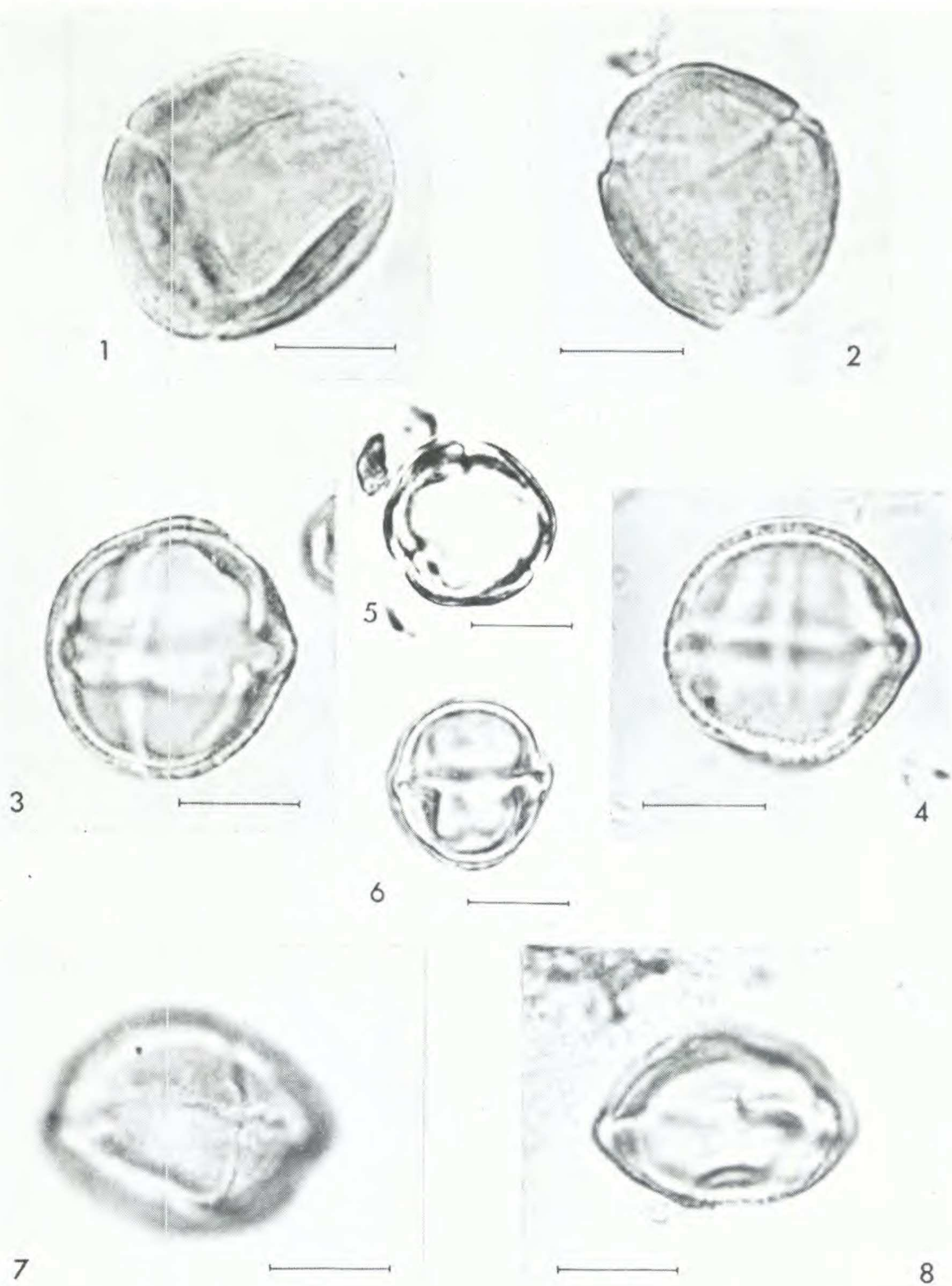
Although pollen of all of these species of *Rhizophora* is quite similar and pollen of each species shows morphological variation, the species can be separated to some extent. Pollen of *R. Mangle* is quite distinct from that of all the other species except some grains of *R. samoensis*. Typical, well-formed pollen of *R. samoensis* is also distinct from that of the other species, with the exception of some grains which, as stated above, may be confused with those of *R. Mangle*. Crumpled grains of *R. samoensis* are similar to some grains of *R. Harrisonii*.

Pollen of *R. racemosa* is distinctive in being oblate-spheroidal, and thus cannot be mistaken for pollen of any of the other types, except for that of some grains of *R. Harrisonii*. Modern pollen of *R. Harrisonii* has not been abundantly available. In order to determine whether the pollen of *R. Harrisonii* is distinctive and clearly distinguishable from the other species, much more flowering material is needed. In addition, further taxonomic work is needed on the entire genus to determine if the presently disputed species boundaries can be more clearly defined. Until such work is completed, it will remain somewhat hazardous to make species determinations of fossil *Rhizophora* grains on a statistical basis.

Fossil Rhizophora Pollen

On the basis of morphology as described above, the fossil *Rhizophora* pollen has been divided into two major groups which reflect not only the pollen morphology but also the division of the species of *Rhizophora* into two groups occupying somewhat different habitats. The first is composed of typical *R. Mangle*-type and *R. samoensis*-

PLATE XL



Modern and fossil *Rhizophora* pollen types. 1, *Rhizophora racemosa*, modern; polar view. 2, *Rhizophora racemosa*-type; fossil, Simojovel; polar view. 3, *Rhizophora Mangle*, modern; equatorial view. 4, *Rhizophora Mangle*-type; fossil, Simojovel; equatorial view. 5, *Rhizophora* sp.; fossil, Simojovel; polar view. 6, *Rhizophora Mangle*-type; fossil, Mina Palo Blanco; equatorial view. 7, *Rhizophora racemosa*, modern; equatorial view. 8, *Rhizophora racemosa*-type; fossil, Simojovel; equatorial view. The scale on each figure is 10 μ .

type pollen, and will be designated as *R. Mangle*-type.⁵ The second consists of pollen of *R. racemosa*-type and *R. Harrisonii*-type and will be designated as *Rhizophora*-spp. In this group are included fossil *Rhizophora* grains present in very small quantities in several of the fossil samples which resemble those of *R. Harrisonii* but which are not completely distinct from somewhat crumpled grains of *R. samoensis*. Since these grains occur consistently together with high percentages of *R. racemosa*-type and *R. Harrisonii*-type, and decrease in percentage as *R. Mangle*-type increases, their affinity is probably with the former group. The category “*Rhizophora* affinity uncertain” was established to include grains which, due to poor preservation or unfavorable orientation, could not be placed with certainty in one of the major categories.

It is not proposed in this study to attempt a rigorous statistical treatment of the observed *Rhizophora* pollen nor to identify minor components of this pollen flora. An initial investigation of the slides indicated that a count of 200 grains per sample was sufficient to suggest the major outlines of the vegetation and the relative frequencies of the most abundant pollen types. For this purpose, slides were scanned at 300×. Final determinations were made at higher magnifications. The first 200 identifiable pollen grains were recorded. Record was kept also of the relative percentages of pollen and fungal spores in each sample. Data concerning the relative abundances of different *Rhizophora* pollen types and of

⁵ Nomenclature of the fossil pollen follows the principles outlined by Zagwijn (1960). As summarized by Muller (1964, p. 35), these may be stated as follows: “If a fossil pollen type has been assigned to a given natural taxon, this expresses the author’s confidence in a high degree of probability for the identification. If, however, the word “-type” is added this means that the pollen type is known to occur also in a related taxon of the same rank.”

fungus spores compared with total pollen, are summarized in Table I. The significance of these percentages is discussed in a following section.

THE ECOLOGY OF MODERN MANGROVE AND ASSOCIATED VEGETATION

The term "mangrove" is applied both to the physiognomically similar but taxonomically diverse group of salt-tolerant semi-aquatic woody plants that grows along silted shorelines and in brackish water throughout the tropics and to any member of this vegetation. The New World mangrove association includes four major genera: *Rhizophora*, *Avicennia*, *Laguncularia* and *Conocarpus*. Of these, only *Rhizophora* and *Avicennia* have more than one species. An additional minor component of mangrove vegetation on the west coast of Central and South America is *Pelliciera rhizophorae* Pl. & Tr. Some workers would also include as "mangroves" plants with a limited salt tolerance that occur in swamps behind the "true mangroves", e.g., *Cassipourea* (Cuatrecasas, 1958).

The ecology of New World mangroves has been studied by Chapman (1939), Cuatrecasas (1958) and others. Lindeman (1953) has given a complete description of the vegetation types of coastal Surinam, including the mangrove, which is extended by Muller (1959) and van der Hammen (1963) to the north coasts of Venezuela and British Guiana. Cuatrecasas (1958) has described the situation along the coasts of Colombia and Ecuador. Only brief descriptions of mangrove vegetation are available for Mexico and Central America.

Studies of recent pollen sedimentation by Muller (1959, 1964), van der Hammen (1963) and Spackman, *et al.* (1964) indicate that, among the mangroves, only species of *Rhizophora* and *Avicennia* are likely to be represented in the pollen record to any great extent. Thus,

TABLE I. Relative abundance of *Rhizophora* pollen types and fungal spores.
Explanation: np – not present; p – present in negligible amounts.

Sample Number and Locality	% $\frac{\text{Rhizophora}}{\text{total pollen}}$	% $\frac{\text{R. Mangle-type}}{\text{total Rhizophora}}$	% $\frac{\text{Rhizophora spp.}}{\text{total Rhizophora}}$	% $\frac{\text{Rhiz. aff. uncertain}}{\text{total Rhizophora}}$	% $\frac{\text{fungal spores}}{\text{total pollen}}$
I Simojovel	90	p	85	15	10
II Mazantic	66	p	40	60	10
III Pabuchil	45	20	40	40	111
IV Huitiupan	45	15	50	35	62
V Portugal #1	30	np	95	p	100
VI Portugal #2	40	np	75	25	37
VII Las Cruces	p	np	np	p	np
VIII Palo Blanco #1	50	np	35	65	16
IX Palo Blanco #2	75	5	35	40	38
X Naranjo #1	6	np	20	80	14
XI Naranjo #2	16	np	20	80	54
XII Jolpabuchil	p	np	np	p	np

any palynological interpretation of mangrove vegetation rests likewise primarily upon reconstruction of conditions indicated by these two genera, and particularly by *Rhizophora*, the most abundant pollen source. More studies on present-day pollen sedimentation are needed before anything other than very general ecological conclusions may be reached. However, the various species of *Rhizophora* do provide significant, although considerably limited, ecological data. The abundant incorporation of *Rhizophora* pollen into sediments is a result, in part, of the manner in which the pollen is released. Rhizophoras produce a large amount of small light pollen which is released into the bud before anthesis and much of which is retained by the hairy petals and is not blown away or carried by insects when the bud opens. Both the anthers and the petals fall from the trees into the water within two or three days after the bud opens, carrying the pollen directly into the water (Guppy, 1906).

Rhizophoras are well adapted to growth in regions of extreme tides, because of the ability of the viviparous seedlings to root rapidly and to withstand inundation. Under these tidal conditions, it forms broad bands along the western coast of South America. Where tides are of low amplitude, for example along the north coast of South America, *Rhizophora* may be scarce or absent along the coast.

Rhizophora Mangle (red mangrove), the most widespread species, is a pioneer which establishes itself successfully on unconsolidated silt if its seedlings are left unflooded for as little as 48 hours. It appears to be the most salt-tolerant of the New World mangroves, occurring both on the open sea shore (if protected from extreme wave action) and in areas where salt concentrations in the soil are abnormally high due to periodic flooding and evaporation (Guppy, 1906; Savory, 1953; Jonker,

1959). Its luxuriant growth in such areas as southern Florida, however, indicates that it does not always require this high salinity. Here, the usual species found in more brackish water are absent.

Rhizophora Harrisonii, the second most widespread of the species, is characteristic of brackish estuaries and rivers in West Africa, on both the east and west sides of the South American continent and on the west coast of lower Central America. The tree forms great expanses of tall forest bordering the rivers in Surinam (Jonker, 1959).

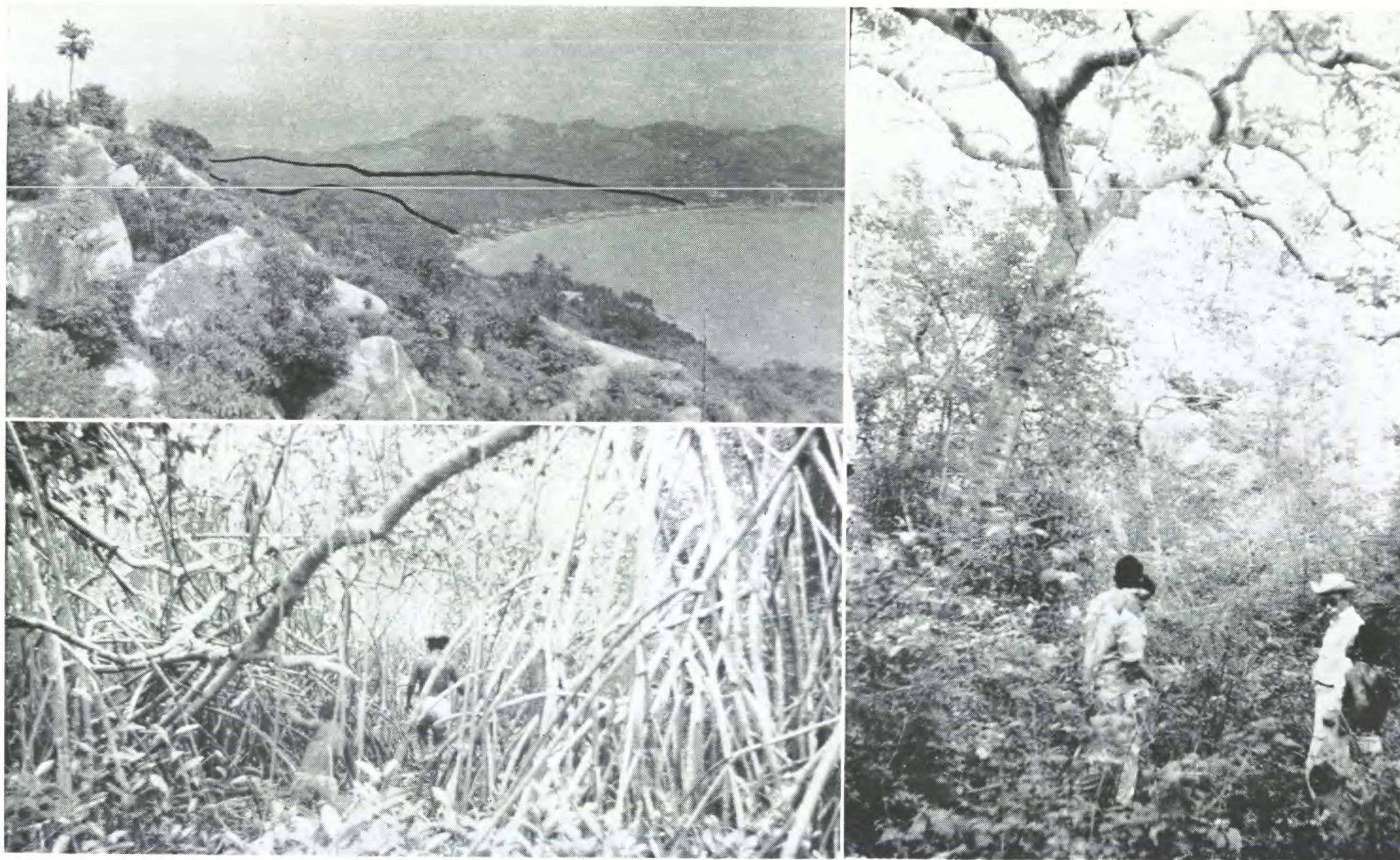
Rhizophora racemosa is more restricted, the species having never been found on the west coast of the Americas. *R. racemosa* is considered the least salt-tolerant of the *Rhizophoras*, and it is found far up tidal rivers, growing together with *R. Harrisonii* and beyond the range of that species into nearly fresh water. Both Savory (1953) and Jonker (1959) consider it the least salt-tolerant of the *Rhizophora* species.

The species occurring on higher ground within or near the mangrove and in fresh-water swamps behind or upstream from the mangroves vary from region to region. In the coastal regions of Surinam, Venezuela and British Guiana, where *Avicennia* is the dominant mangrove, the region behind the mangrove belt is a complex mosaic of vegetation types controlled by local soil and water conditions. Especially important is the mixed swamp forest (including *Pachira (Bombax) aquatica* and *Pterocarpus officinalis*) which may form extensive stands behind the mangroves. There also are often palm swamps; herbaceous swamps, often dominated over great expanses by ferns (e.g., *Acrostichum aureum*); as well as special vegetation types on sandy beach ridges and high natural levees. This pattern is very different from that described by Cuatrecasas and others for the west coast of South

America. Here, behind the *Rhizophora* zone, the back-swamp vegetation is usually a mixed swamp forest type which forms a gradual transition to rain forest. In Mexico and some other areas of Central America, where hills come down to the shore, such a transition belt is usually narrow or absent.

As previously noted, *Hymenaea Courbaril* today frequently occurs in habitats closely associated with mangroves along the Pacific coast of Central America. This has been observed by the senior author along the Guerrero coast in Mexico and along the Osa Peninsula in Costa Rica. Lindeman (1953) also has reported *H. Courbaril* as occurring in Surinam on low sand ridges near the mangroves.

The most significant present-day situation observed by the senior author that might represent possible site conditions like one of those in which the Chiapas amber could have been deposited occurs around Puerto Márques Bay, Guerrero, Mexico. Here, *H. Courbaril* is one of the dominant trees in a Tall-Medium Subdeciduous forest-type (Miranda and Hernández-X, 1963) on the hills sloping either to the ocean or to bays (Plate XLI). *Hymenaea* occurs along rivers that enter the lagoons and also on sandy ridges that interdigitate into the lagoon (Plate XLI). These lagoons are fringed primarily by *R. Mangle* and on higher ground by *Laguncularia racemosa* (Plate XLI). *Hymenaea* also may be found on dune and beach ridge vegetation along the coast in Guerrero and Oaxaca. Around Puerto Márquez Bay, it is easy to visualize how resin from *H. Courbaril* would be deposited into the lagoon with fringing mangroves. A single severe flooding could wash away resin collected in the soil, and the stilt roots of *Rhizophora* offer an excellent mechanism to "trap" the resin. Also, resin may easily be transported down rivers that enter the bays and



(Top, left) Puerto Márquez Bay, Guerrero, Mexico, with *Hymenaea Courbaril* as one of the dominant trees in hillside vegetation. Mangrove vegetation along lagoons is outlined. *Hymenaea* also occurs on sandy ridges extending into the lagoons. (Right) *Hymenaea Courbaril* L. on sandy ridges about 200 yards from lagoonal mangrove swamp shown in top, left. (Bottom, left) Typical *Rhizophora Mangle* stilt roots occurring in Puerto Márquez mangrove swamp with *Hymenaea Courbaril* on adjacent sand ridge.

lagoons, for it was frequently observed that soil around the bases of streamside *Hymenaea*, where resin often accumulates, has been washed away, exposing the roots. In general, it has been observed that present-day habitats of *H. Courbaril* offer a number of possibilities for resin to be deposited in a site dominated by mangrove vegetation.

Interpretation of Rhizophora Pollen Data from Amber-bearing Sediments

Muller (1959) studied the pollen of mangrove and associated vegetation in sediments of the Orinoco delta and the Gulf of Paria near Trinidad. He was also able to define palynological provinces in these sediments on the basis of pollen composition and abundance. He has shown that the major factor influencing pollen deposition there is water transportation. He further points out that pollen studies may be of use in facies determination and reconstruction of ancient basins of sedimentation. Van der Hammen (1963) extends Muller's observations and concludes the following in regard to deposition of mangrove pollen in British Guiana (pp. 140-141):

1) "In a Mangrove forest the percentage of *Rhizophora* + *Avicennia* may be between 45 and 95%. If the Mangrove forest forms only a narrow fringe, the sediment tends to have lower percentage, as for instance 30."

2) "Mud deposited in front of the coast-line, may have percentages of *Rhizophora* + *Avicennia* pollen of 30-50%. Further offshore the percentage of *Rhizophora* pollen increases and may be up to 70% or more."

3) "Swamp forests immediately behind the Mangrove forest may have 45-10% (or less) and Swamp forests farther inland may have 10-0% *Rhizophora* pollen in the sediment."

4) "Heavy pollen grains. . . rarely are found in sediments in front of the coastline in any appreciable percentage. Lighter pollen grains are carried seawards more easily and may be sedimented at considerable distance from the shore."

5) "The Fungi spore content is in general highest in the swamp and forest area behind the coast-line and ranges between 10 and 100% of the pollen sum, although both higher and lower values may occur (0-500%). In the Mangrove belt the percentages are usually relatively low, ordinarily varying between 3 and 10%. In a zone in front of the coast percentages are generally low (1-3%), and spores of this type are not found farther offshore."

Although Muller's and van der Hammen's conclusions cannot necessarily be assumed to represent conditions along the Central American coasts, they provide a tentative framework for interpretation of the Chiapas sediments. Pertinent palynological data from these sediments are summarized in Table I. The relationship of *Rhizophora* pollen to total pollen content of the sediments is represented by "percent *Rhizophora* pollen." "Total *Rhizophora*" constitutes the sum of all *Rhizophora* types as well as those with uncertain affinities. In an attempt to gain more detailed ecological information from the total *Rhizophora* category, it was divided into three groups. The *R. Mangle*-type which, as established by ecological studies of modern mangroves, represents pollen of the species occupying a more saline habitat; *Rhizophora* spp. (*R. racemosa*-type and *R. Harrisonii*-type) which represents pollen of the species living in less saline (brackish and fresh) habitats; and *Rhizophora* with uncertain affinities. The percentage relationship of each of the first two groups to the total *Rhizophora* pollen, therefore, gives a possible indication of a more saline or

more brackish environment. However, this conclusion must remain tentative, until statistical analyses are undertaken of *Rhizophora* pollen presently being deposited in various types of marine and brackish environments, to show whether the relative percentages of the two types of pollen actually reflect the two vegetational groups. The percentage of fungal spores to total pollen is considered by van der Hammen to represent a possible index of "landinwards" conditions. Since the identification of individual grains as belonging to the *Rhizophora Mangle*-type or *Rhizophora* spp.-type may not always be certain, a few grains in each sample may have been misidentified. Therefore, percentages given in Table I are approximate.

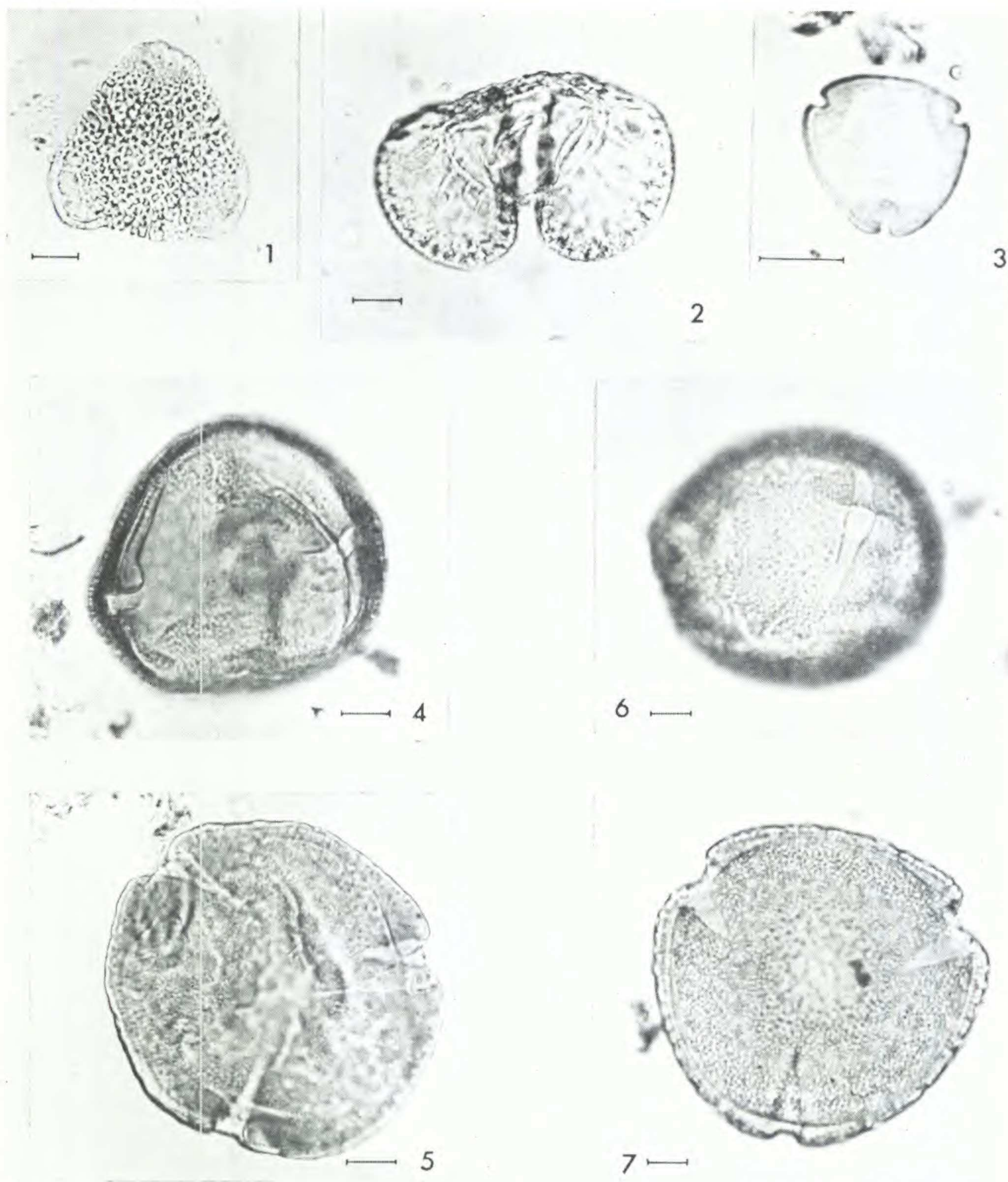
Sample I from Simojovel appears from several lines of evidence to represent deposition at the actual site of a mangrove swamp. The sample is lignitic in nature, and mangroves today are known to be active peat formers (Chapman, 1939; Spackman *et al.*, 1964). The total content of *Rhizophora* pollen is very high (90%); associated pollen is large and heavy, and would not be expected to be carried far from its source plant. The fungal spore content is very low. The extremely high percentage of *Rhizophora* pollen also suggests that the source area was not a narrow fringing mangrove but an extensive forest. *Rhizophora Mangle*-type is present (Plate XL, fig. 4), but in negligible percentages, suggesting that the mangrove forest here was composed largely of individuals belonging to the *Rhizophora* spp. division (Plate XL, figs. 2 and 8) and grew perhaps under brackish conditions. The occurrence in this sample of pollen very closely resembling that of *Pelliciera rhizophorae* (Plate XLII, figs. 4-7), a highly specialized member of the Theaceae, is very interesting. Since the range of this monotypic genus today is restricted to mangrove swamps along the Pacific coast from Costa Rica south to western Colombia

(Johnston, 1949), its presence in this sample suggests a wider distribution in the past.

Sample II, Mazantic, is very closely related to that from Simojovel (I) in lithology. Approximately 66% of the grains are recognizable as *Rhizophora*. Although poor preservation of the sample made division of the grains into the two major *Rhizophora* categories difficult and somewhat uncertain, a large proportion of the grains could be assigned to the *Rhizophora* spp. group. *R. Mangle*-type was present only in very low percentages; the same is true for fungal spores. From the general similarity of the two sediments, it is suggested that the samples from Simojovel and Mazantic represent a similar habitat.

Samples III and IV, from Pabuchil and Huitiupan, although somewhat different lithologically, appear to be comparable palynologically. In both, nearly half of the pollen (45%) encountered is of the *Rhizophora* type. Of this, a comparatively large percentage (20%) is definitely *R. Mangle*-type. The category *Rhizophora* affinity uncertain here includes a number of grains referable probably to *R. Mangle*-type, seen in polar view. Such grains were placed in this category, since it is often difficult to distinguish modern *R. Mangle* in this orientation from other species. In both samples, fungal spores are abundant with respect to the total pollen. Other microfossils include pollen very closely resembling that of *Engelhardtia* (Plate XLII, fig. 3), a very low percentage of pollen of the *Pelliciera*-type, and a few Hystrichosphaerids in the Huitiupan sample. The two are similar in the percentages of unidentified tricolporate and monocolpate pollen; marine shells occur in both samples. These samples represent probably similar habitats. By van der Hammen's criteria, the relatively high fungal spore content suggests that the site was very near the coastline,

PLATE XLII



Miscellaneous fossil pollen types associated with *Rhizophora*. 1, *Pachira*-type; fossil, Portugal. 2, *Podocarpus* sp., fossil, Pabuchil. 3, *Englehardtia* sp., fossil, Pabuchil. 4, *Pelliciera*-type; fossil, Simojovel; equatorial view. 5, *Pelliciera*-type; fossil, Simojovel; polar view. 6, *Pelliciera rhizophorae*; modern. 7, *Pelliciera rhizophorae*; modern. The scale on each figure is 10 μ .

just behind, or perhaps just offshore; the presence of large, heavy grains also supports this. The relatively high percentage of mangrove pollen suggests that a mixed *Rhizophora* swamp was present in the vicinity. The higher percentage of *R. Mangle*-type pollen and the marine shells may indicate more coastal conditions than those suggested by samples I and II.

The two samples from Portugal (V and VI) are similar in lithology and in the presence of moderate percentages of *Rhizophora* pollen which is referable to the *Rhizophora* spp. division. The majority of the pollen is made up of various unidentified tricolpate and monocolpate pollen. Small quantities (3–7%) of *Engelhardtia*-type grain occur. Sample VI contains several interesting non-rhizophoroid grains, among them large planar tetrads comparable to those of the Annonaceae and a grain of *Pachira aquatica* Aubl., a member of the Bombacaceae today characteristic of fresh-water swamp regions behind the mangrove as well as of streamsides. On the basis of these non-rhizophoroid grains, these samples would appear to represent a somewhat less brackish facies than any of the above and suggest deposition in a swamp forest adjacent to mangroves. However, the presence of marine fossils in the same samples casts some doubt on this interpretation.

Pollen in Sample VII, a coarse-grained siltstone from the Las Cruces slide, was infrequent and poorly preserved. Those grains encountered appeared to be *Rhizophora*, perhaps of the *Rhizophora* spp.-type. A relatively large piece of amber, however, from Las Cruces has oysters embedded in the surface, indicating that the resin was still soft when it entered the marine environment. This suggests either that the trees producing the resin were growing along the shore or that the resin was transported only a short distance before the shells were caught in it.

The two samples from Palo Blanco (VIII and IX) are generally similar. Sample VIII is from the bed immediately underlying that of Sample IX and appears to contain no *R. Mangle*-type, and though there is much uncertainty about the affinity of many individual grains due to poor preservation, it is improbable that a significant number *R. Mangle*-type have been overlooked. *Engelhardtia*-type makes up 22% of the total recognizable pollen. The genus *Engelhardtia* today is restricted to the highland areas of Mexico and Central America (Miranda and Sharp, 1950), and to southeast Asia, where it is common in the hills of coastal regions (S. Hu, pers. comm., 1965). The abundance of grains of this type in the Chiapas sediments (and in other early Tertiary sediments, cf. Traverse, *Engelhardtia Spackmanii*) suggests either that the grain represents an extinct line with pollen very similar to the modern *Engelhardtia*, or that the genus has changed both its range and ecological preference in the New World since the Oligo-Miocene. Sample IX contains a small percentage of unmistakable *Rhizophora Mangle*-type pollen and a number of *Rhizophora* affinity uncertain grains which belong probably to *R. Mangle* and also 7% *Engelhardtia*. The matrix of both samples contained glauconite and marine fossils. The high percentage of *Rhizophora* pollen and the presence of fungal spores suggest deposition in the vicinity of mangrove vegetation. There is some carbonized material which might result from re-deposition of older material, as is known to occur in levee deposits in the Orinoco delta (Muller, 1959). However, percentages of *Rhizophora* and other small, light pollen are known to increase also in sediments quite distant from shore. Most of the grains encountered in these sediments are in the 20–40 μ size range and indicate possibly an offshore depositional environment.

The samples from Mina de Naranjo (X and XI) are presumed to be roughly the same age as in the Mina Palo Blanco sediments. Samples X and XI are similar in the relatively low percentages of *Rhizophora* pollen present and in their poor preservation. Only a few grains in each sediment could be confidently placed in one of the two major divisions. The remainder were placed with those of uncertain affinity, but most grains belong probably to the *Rhizophora* spp. group. In Sample X, fungal spores were present in low percentages, and the majority of the pollen were unidentified tricolpate and monocolpate types. There were 7% fern spores. Pollen of *Podocarpus* (Plate XLII, fig. 2) occurs infrequently in these sediments. *Podocarpus* is the only conifer present, other than a few poorly preserved grains probably of *Pinus*. Sample XI contained a somewhat larger percentage of *Rhizophora* pollen, including a number of *Rhizophora* spp.-type grains, and a considerably larger percentage of fungal spores. The percentage of *Engelhardtia*-type decreased to 3%, and the number of fern spores remained high (7%). The depositional environment of these samples is not suggested on the basis of their pollen content. The low percentages of *Rhizophora* might be interpreted as indicative of deltaic deposits such as those investigated by Muller (1959, Pica E), or of foreshore deposits. The generally moderate to high percentages of fungal spores in these sediments and the Palo Blanco samples above, according to the ideas of van der Hammen (1963), seem higher than those which would be expected in an offshore environment; many more data from modern depositional environments, however, are needed here. Amber from these deposits does have impressions of marine gastropods, which again suggests that the resin-producing trees were close to the shore so that the resin was deposited in the water (or on the strand line with the shells) before it hardened.

Sample XII, from Jolpabuchil, contained relatively small amounts of poorly preserved pollen and great quantities of carbonized debris, which might perhaps have been re-deposited material. Recognizable tracheids of the sort described by Muller (1959) as re-deposited from Eocene sediments in Venezuela were frequently encountered. Pollen grains included some *Rhizophora* of uncertain affinity. The presence of marine fossils indicates probably an offshore environment.

SUMMARY AND CONCLUSIONS

Pollen from 12 rock samples from Chiapas, Mexico, either from strata containing amber or immediately adjacent to them, were studied. These samples do not vary greatly in lithology, ranging from calcareous siltstone or silty shale to calcareous sandstone. They are all from strata considered to be latest Oligocene or earliest Miocene in age and represent apparently a relatively small interval of geological time. The palynological data indicate development of mangrove vegetation of considerable complexity at or close to the site of deposition of the amber. The most important elements of the vegetation from the standpoint of the pollen record were members of the genus *Rhizophora*, in all probability representing several species of different ecological preferences. Although only one other genus known to be a member of the New World mangrove association today (i.e., *Pellíciera*) was encountered, the possible presence of others is not precluded. As studies by Muller (1959), van der Hammen (1963) and Spackman *et al.* (1964) have indicated, other mangroves such as *Laguncularia* and *Conocarpus* may be present, but only *Rhizophora* and *Avicennia* pollen commonly occur in abundance in recent sediments. Until more careful studies of the delimitation of different mangrove species and their pollen are made,

and investigation of pollen sedimentation on the Central American coasts is carried out, all paleoecological conclusions regarding the Chiapas mangrove association must be tentative.

Despite the fact that it is not possible from presently available data to reconstruct the vegetation types at or close to the depositional site of the amber, certain environmental conditions are strongly suggested. It appears that, at certain sites, the beds from which the samples came were deposited under brackish conditions with a predominance of *Rhizophora* (Simojovel and Mazantic); in others, in a more coastal, saline mixed *Rhizophora* vegetation (Pabuchil and Huitiupan); in somewhat less brackish conditions, suggesting deposition in or near a backswamp forest adjacent to *Rhizophora* (Portugal); or possibly in foreshore conditions in the vicinity of mangroves (Mina Palo Blanco and Mina de Naranjo). These data likewise support the geological evidence that deposition of the amber-bearing beds took place, in general, along a coastline of a shallow, tropical sea with occasional shoreline fluctuations. Evidence that the amber was produced by possible ancestral populations of *Hymenaea Courbaril* also receives corroboration, as this species today commonly occurs in habitats in which the resin produced could easily enter mangrove deposits. Likewise, the significant absence of *Pinus* in the amber-bearing beds, except for a rare, eroded specimen, seems to support a source tree other than pine. Since pine produces such large quantities of pollen that get widely distributed by wind, its scarcity tends to indicate that pines were probably not present within this vicinity.

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APPENDIX

Following is a brief lithologic description of the samples studied. Locality numbers in parentheses with "B" and "D" prefixes refer to materials on loan to the Botanical Museum of Harvard University from collections of the University of California Museum of Paleontology. Locality numbers with "Pl" prefixes are in the Harvard University Paleobotanical collections.

Sample I (D-621) was collected from the landslide on the east side of the village of Simojovel. It is a brownish to reddish, coarse-grained siltstone, including fine seams of lignitic material.

Sample II (Pl-32) was collected upstream from Mazantic from a 5-10 foot lignitic bed containing amber.

Sample III (Pl-7) was collected from Pabuchil (Rancho Alegre) slide two miles northwest of Simojovel. It is a sandy, dark-grey calcareous silt stone from an amber-bearing interval with marine fossils.

Sample IV (Pl-8) was collected at an outcrop along the road to Huitiupan. It is a leached calcareous sandstone with carbonaceous sandstone with carbonaceous streaks and contained fairly abundant amber.

Sample V (B-4178) was collected at the Portugal (also known as Santa Catarina) slide on the north side of the Río Ancora valley. It is a greyish-brown siltstone containing marine fossils from a bed immediately below the amber-bearing strata.

Sample VI (B-4177) also was collected at Portugal slide from a blue silty clay 100 feet in the section above Sample V and 4-5 feet above a thin lignitic zone.

Sample VII (Pl-33) was collected at the Las Cruces slide about 15 miles southeast of Simojovel. It is a brownish, coarse-grained siltstone with some lignitic material, from a 4-8 foot lignitic interval immediately above beds containing amber.

Sample VIII (D-614) was collected from a marine glauconitic sandy shale at Mina Palo Blanco, Finca La Primavera on the San Pedro River northwest of Simojovel.

Sample IX (D-615) was collected from a marine black silty-shale at Mina Palo Blanco from the bed immediately above the previous sample.

Sample X (B-8106) is a marine glauconitic silty-shale collected at Mina de Naranjo, Finca La Primavera.

Sample XI (B-8105) is a marine glauconitic silty-shale collected at Mina de Naranjo.

Sample XII (B-4180) was collected at Jolpabuchil. It is a greyish-black carbonaceous siltstone with marine fossils.